



CEE review 07-013

WHAT ARE THE MECHANISMS OF REGENERATION POST-DISTURBANCE IN TROPICAL DRY FOREST?

Systematic Review

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Draft protocol published on website: 7 December 2007- Final protocol published on website: 4 July 2008 - Draft review published on website: 21 December 2009 – Final review posted on website: 3 June 2010

Cite as: McDonald, M. A., McLaren, K. P., and Newton, A. C. 2010. What are the mechanisms of regeneration post-disturbance in tropical dry forest? CEE review 07-013 (SR37). Environmental Evidence: www.environmentalevidence.org/SR37.html

Systematic Review Summary

Background

Tropical or subtropical dry forests originally accounted for around 42% of total global forest cover (Murphy and Lugo, 1986), but a review by Miles et al. (2006) estimated the current extent of tropical dry forests to be just 1,050,000 km². According to the FAO Global Forest Resources Assessment (2005), total global forest cover is currently around 40,000,000 km². Thus, tropical dry forest now only accounts for around 2.5% of total global forest cover, and virtually all of the dry forests that remain are currently exposed to a variety of different threats, largely resulting from human activity. Their mode of regeneration and resilience to disturbance is not well understood, but moisture availability plays a critical role. Vegetative regeneration may be the primary regeneration mechanism in disturbed dry forest sites where resprouting offers considerable resilience when successful regeneration by seed is highly susceptible to rainfall seasonality. Selective pressure favouring resprouting may also be related to the intensity and frequency of natural disturbances, or any canopy-opening factor that might result in heavier drought stress and mortality of seedlings. The sensitivity to moisture availability renders the regeneration of the dry forests highly vulnerable to predicted climate change effects.

Objectives

We conducted a systematic global review of the mechanisms of recovery of tropical dry forests after disturbance, in order to achieve an understanding of how tropical dry forests might best be restored.

Methods

Multiple electronic databases were searched using *a priori* search terms. In addition, electronic communications were made to individual experts, forest departments and research institutions. Studies were considered for inclusion if they contained data on modes of regeneration after disturbance, or provided evidence of facilitation. For each study considered, the study characteristics (location, climate, experimental design, nature of intervention and comparators and outcomes measured), sources of heterogeneity and main results were recorded. Two distinct sets of observation were recorded *a posteriori*: i) regeneration method post-disturbance (regeneration composition by seeds or vegetative sprouting ii) evidence of facilitation (seedling survival under forest canopy or in gaps).

Main Results

The initial systematic literature identified in excess of 10,000 articles of potential relevance. This was reduced to 534 on the basis of title. Reviewers' comments on the draft protocol advised two additional search terms (drought and dry season length) which yielded a further 545 articles, of which 56 were duplicated in the initial list. Thus, 1023 articles were finally considered on the basis of title and abstract. Of these, the full text of 35 articles was assessed and 16 articles were retained for further analyses. Of these, 14 considered regeneration post-disturbance, and 2 considered

facilitative effects of the forest canopy. The studies varied widely in the time since disturbance, and the intensity of disturbance. There was also a dearth of studies which considered seedling or sprout origins of individuals in the undisturbed forest against those in disturbed forest, and we were restricted to considering a gradient of intensity of disturbance as a comparator. This departed from the terms of the protocol and limited more detailed meta-analyses of the data. Only two studies considered the facilitative effects of the canopy and were not included in any analyses.

Conclusions

In the range of forests studied, and across the climates and location, the response of forests to disturbance was sufficiently consistent to allow for general conclusions about their mode of recovery. Along a gradient of disturbance, it seems to be the case that following recent disturbance events, resprouts are the most prevalent individuals. When disturbance has taken place over a longer interval, individuals of seedling origin become more important in forest composition. As rainfall increases, the proportion of regeneration accounted by seedlings increases, while the proportion of coppicing individuals decreases, following cutting. However, an equal contribution by seedlings and shoots to regeneration following cutting is expected to occur at sites with a total annual rainfall of 1400 mm or more and approximately 19 - 20 years following cutting. Burning, on average reduced the predicted time at which the contribution from both seedlings and coppice will be equal (7 - 10 yrs), and the total annual rainfall at which this will occur (approximately 1150 mm/year). The implications for dry forest restoration would appear to be that initial regeneration by sprouting is most important which will affect both species and genetic diversity in the short term, but providing that further disturbance is restricted, new seedling regeneration will occur. Burning will affect both species and genetic diversity, and future seed sources. The implications from a research perspective are that results such as these could be used to develop more generic models of dry forest regeneration patterns which will enhance our ability to restore these threatened ecosystems. We need more climate change and regeneration studies in dry forest ecosystems, so that a comprehensive theory and explanation of dry forest dynamics can be built to afford greater understanding of the process and mechanisms governing regeneration in the dry tropics, this has been largely achieved for temperate and tropical rainforest ecosystems, but is as yet under-developed for tropical dry forests.

1. Background

It is estimated that of the total global extent of tropical forest, tropical or subtropical dry forest accounts for 42 % of total global forest cover (Murphy and Lugo, 1986). They have been exposed to severe, large-scale changes, through the cutting of valuable trees, creation of pastures, accidental or intentional fires (Gerhardt and Hytteborn, 1992) and as a source of fuel wood (Murphy and Lugo, 1986) and virtually all of the tropical dry forests that remain are currently exposed to a variety of different threats, largely resulting from human activity (Miles et al., 2006). However, despite their over-exploitation there have been relatively few studies of tropical dry forest and even fewer studies done on their regeneration pathways, which can provide knowledge crucial to the restoration of these forests (Vieira and Scariot, 2006).

Tropical dry forests have particular natural regeneration attributes which are not currently well understood (McLaren and McDonald, 2003b; Vieira and Scariot, 2006). Unlike tropical moist forests, regeneration in gaps is not the primary mechanism; and the availability of moisture plays a major role in successful establishment of seedlings. The timing and duration of rainfall is crucial as there is a high probability that a given seedling will be left stranded in a drying soil and there is therefore a low probability of successful regeneration from seeds (Ewel, 1980). The pronounced seasonality affects patterns of seed production, germination, survival and seedling development (Khurana and Singh, 2000). Seeds of a majority of dry tropical species mature in the dry season and they are dispersed at the beginning of the rainy season when sufficient moisture is available for germination and seedling growth (Singh and Singh, 1992; McLaren and McDonald, 2005). The favourable growing period is restricted to short rainy seasons when seeds are expected to germinate and seedlings establish. The deciduous state of some or most tree species allows for an increase in irradiance that in the absence of moisture exacerbates desiccation in seedlings and hence higher rates of mortality (e.g. Gerhardt, 1996a).

Vegetative regeneration may well be the primary regeneration mechanism in disturbed dry forest sites, where stem and roots remain in place (Ewel, 1977; Murphy and Lugo, 1986; Murphy et al., 1995; McLaren and McDonald, 2003b). In the wet tropics, where large-scale disturbance occurs as a result of clearing, burning and extensive storm damage, regeneration from stem coppice is also important (e.g. Byer and Weaver, 1977; Ewel, 1977; Stocker, 1981; Uhl et al., 1981; Putz and Brokaw, 1989; Kauffman, 1991; Bellingham et al. 1994). It may however, be more important in dry forest sites where resprouting offers considerable resilience to disturbance in dry forests where successful regeneration by seed is highly susceptible to rainfall seasonality (Ky-Dembele et al., 2007; McLaren and McDonald, 2003c; Vieira et al., 2006; Vieira and Scariot, 2006). Also, because trunk bases are less subject to rapid decay in the dry tropics, trees in seasonally dry forests are much more prone to reproduce vegetatively through coppicing (Ewel, 1980) in response to disturbance. However, the different abilities of species to produce shoots will affect long-term species diversity in disturbed forests. Selective pressure favouring resprouting may also be related to the intensity and frequency of natural disturbances, or any canopy-opening factor that might result in heavier drought stress and mortality of seedlings.

The sensitivity to moisture availability renders the regeneration of the dry forests highly vulnerable to predicted climate change effects. Most predictions of the response of tropical forests to rising CO₂ concentrations and temperatures and changing precipitation patterns have concluded that changes in precipitation will have the most impact, in that drying trends will remove drought-sensitive species from the forest (e.g. Condit, 1998). However, a recent assessment of neotropical rain forests over a 20 year period showed an increase in faster-growing species to the detriment of slower-growing sub-canopy species, apparently irrespective of their light or moisture requirements (Laurance et al., 2004). This may be due to the fertilising effect of rising CO₂ concentrations. However, this is uncertain, and strong droughts have been shown to cause shifts in tree-community composition in Panama (Condit et al., 1996) and niche differentiation with respect to soil water availability has been shown to determine distributions of tropical trees at both local and regional scales (Engelbrecht et al., 2007). Körner (1998) postulated that changing plant water relations could become the most important of all elevated CO₂ effects on tropical forests, as water is always a selective driver of plant growth. The length of dry periods is among the key determinants of the species structure of communities (Condit, 1998; Körner, 1998). 97% of the remaining global dry forest is estimated to be ‘at risk’, and in the Americas this is mostly from climate change (Miles et al., 2006). Most studies on the effects of climate change in the tropics have been centred on tropical rainforest with a noticeable absence of work in tropical dry forest (Körner, 1998). Given that seasonally dry forests are so heavily impacted in the neotropics, and largely surrounded by agricultural landscapes, it is unlikely that they will be able to spread their range in the face of hotter and drier climates because of the lack of habitat in anthropogenic landscapes (Pennington et al., 2004). Mayle et al., (2004) demonstrated that dry forest species merely shift their ranges rather than expand them in the face of drier climates in the Bolivian Chiquitano region. If this is generally true, then the future of the seasonally dry forests is very bleak as they will “die where they stand” (Pennington et al., 2004).

Drying trends in a dry forest environment may create conditions similar to those more usually found in xeric tropical environments where plants are more drought-tolerant and seedling survival is enhanced by both the direct effects of habitat amelioration by shade, and the indirect effects of shaded plants attaining greater size before the onset of extreme conditions (Hastwell and Facelli, 2003). This is regarded as facilitation, the positive effect of plants on the establishment or growth of other plants (Holmgren et al., 1997). In the last decade, plant ecologists have focused more on the occurrence of positive plant-plant interactions than ever before, especially in severe environments. These studies have shown that facilitative effects are stronger in these environments, leaving little doubt of their generality and importance and raising questions about the assumed ubiquity of competition as the dominant interaction between neighbouring plants. Postulated relationships between facilitation and stress (Bertness and Callaway, 1994; Callaway and Walker, 1997) propose that, as conditions for plant growth becomes increasingly adverse, facilitation becomes ‘usually common’ (Bertness and Callaway, 1994) or that the ‘importance’ and intensity of facilitation increases. Dormann and Brooker (2002) suggest a model of plant interactions whereby the importance of facilitation increases along a gradient of increasing environmental harshness, while the importance of competition decreases (Figure 1). They apply this model to harsh environments, such as the Arctic, where species removal experiments tend to find facilitative rather than competitive effects.

This phenomenon has also been recorded in more mesic environments which encounter periods of environmental severity, particularly drought. Hastwell and Facelli (2003) found that the relationship between facilitation and environment severity is more complex than previously thought, as neither the intensity nor the importance of facilitation necessarily increases as conditions become severe. Maestre and Cortina (2004) found that competitive interactions dominated at both extremes of an environmental gradient and suggested that a shift from facilitation to competition under high abiotic stress conditions is likely to occur when the levels of the most limiting resource are so low that the benefits provided by the facilitator cannot overcome its own resource uptake.

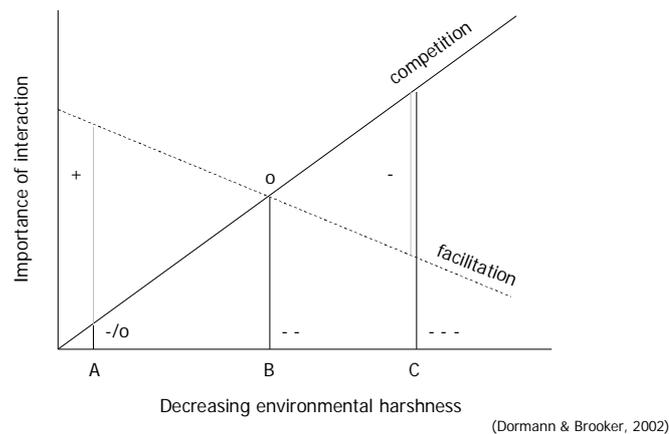


Figure 1. Intensity of facilitation and competition along a gradient of decreasing environmental harshness adopted from Brooker and Callaghan (1998). (A) Facilitation outweighs competition, leading to a negative effect of neighbour removal (grey vertical lines and symbols, indicating positive (+), neutral (o) or negative (-) net effects. In (B) both interactions cancel each other out and in (C) competition is dominant over facilitation, leading to positive effects of neighbour removal.

Thus, the relationship between facilitation and environmental severity is more complex than previously recognised, and clarification of this relationship is central for further progress in plant facilitation research (Brooker et al., 2007). The relationship is likely to be particularly complex in seasonally dry forests in a changing climate where the balance between competition and facilitation is confounded by a decrease in stomatal conductance and increased water use efficiency in response to increasing CO₂ concentrations (Lewis et al., 2004). McLaren and McDonald (2003a) observed that, in shaded plots, seedling density and survival were higher than in unshaded plots, also reflected in higher mortality rates in the unshaded plots. However, competition for moisture between adult trees and seedlings was indicated in the shaded plots by negative growth rates in the seedlings, and mortality in the shaded plots was observed to be higher in the wet season. Thus, it would appear that the facilitative effects of the canopy are stronger in drier periods, and that alleviation of the moisture stress switches the effect of the interaction from facilitative to competitive (Holmgren et al., 1997; McLaren and McDonald, 2003a). A number of other studies have confirmed the importance of shading on tree seedling survival in dry tropical forests where shading significantly improved dry season survival (Gerhardt, 1993, 1996a,b, 1998; Gerhardt and Fredriksson, 1995, Hammond, 1995; Ray and Brown, 1995; McLaren and

McDonald, 2003b). However, the advantages of being below the canopy at a given location may change with seasonal or transient weather conditions (Greenlee and Callaway, 1996; Tielbörger and Kadmon, 2000; Hastwell and Facelli, 2003; McLaren and McDonald, 2003b). Smith and Huston (1989) hypothesized that the response of plants to the combined effects of irradiance (Photosynthetic Active Radiation (PAR)) and water is characterized by a trade-off between drought tolerance and shade tolerance. They proposed a trade-off model, which they used to predict the growth and survival of plants along gradients of PAR and water availability. While this model was supported by empirical studies, the results of field studies on one or a few species did not support the hypothesis (e.g. Hastwell and Facelli, 2003; Holmgren, 2000; Sack and Grubb, 2002; Tielbörger and Kadmon, 2000). Holmgren (2000) therefore expressed the need to test the model using a large set of species as an essential next step in understanding positive plant-plant interactions and these data could also be used to explain species' responses to a drying environment. Hence, it is difficult to predict the impact of drying trends on species' interactions in tropical dry forests. Species within these environments are already drought tolerant and facilitation does occur, consequently the importance of facilitation may increase at least up to a certain threshold level of drought (Maestre and Cortina, 2004). As well as reduced consumption and demand for water, differential responses of growth to CO₂ fertilization between species can be predicted (Körner, 1998). How will this then modify or affect the interaction between plants? Different species have different climatic responses, so they will respond individually to climate change. Consequently, not only would one expect biome shifts (e.g. replacement of rainforest by seasonally dry forest or savannah) but also significant reassortment of species within plant communities in response to such changes (Mayle et al., 2004). Furthermore, relatively little is known about how different tropical forest types will respond to future climate changes (Enquist, 2002).

2. Objective of the Review

2.1 Primary question

What is the importance of facilitation and vegetative regrowth in the regeneration of tropical dry forests?

Table 1. Definitions of components of the primary systematic review question

Subject	Intervention	Outcome
Tropical Dry Forests	Disturbance (natural or anthropogenic) <ul style="list-style-type: none"> • Low intensity (e.g. tree fall) • Medium intensity (e.g. logging, partial canopy alteration, charcoal production) 	Regeneration by seedlings: <ol style="list-style-type: none"> 1) Growth rate of Seedlings 2) Percentage of recovery accounted for by seedlings 3) Canopy facilitation Vegetative regrowth: <ol style="list-style-type: none"> 1) average number of shoots per stem 2) percentage of stems with shoots

	<ul style="list-style-type: none"> • High intensity (e.g. hurricanes, clearance for agriculture, fire) <p>Climate change (dry season length)</p>	<p>3) Average diameter or height of shoots 4) Percentage of diameter or height recovered by shoots 5) growth rate of shoots</p> <p>Species regeneration composition</p>
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2.2 Secondary question

The secondary question assessed the relative contribution of either seedlings or vegetative regrowth to the recovery of the site in terms of growth rates, %DBH recovered, %height recovered, %BA recovered, and %of the species recovered, i.e. a direct comparison of which contributed the greatest to the recovery of structure and floristics.

3. Methods

3.1 Search strategy

The following computerised databases and web engines were searched:

1. ISI Web of Knowledge
2. Science Direct
3. Directory of Open Access Journals (DOAJ)
4. Copac
5. Scirus
6. Scopus
7. Index to Theses Online (1970-present)
8. Digital Dissertations Online
9. JSTOR
10. CABI Databases
11. googlescholar.com

Plus, communications to Forestry Departments, Research Institutions and individual experts

The following search terms were used:

1. (Tropical dry forest*) AND facilitation
2. (Tropical dry forest*) AND competition
3. (Tropical dry forest*) AND seed dispersal
4. (Tropical dry forest*) AND regeneration
5. (Tropical dry forest*) AND resprouting
6. (Tropical dry forest*) AND coppicing
7. (Tropical dry forest*) AND burning
8. (Tropical dry forest*) AND climate change

9. (Tropical dry forest*) AND disturbance
10. (Tropical dry forest*) AND carbon dioxide
11. (Tropical dry forest*) AND clearance
12. (Tropical dry forest*) AND herbivory
13. (Tropical dry forest*) AND shifting cultivation
14. (Tropical dry forest*) AND drought
15. (Tropical dry forest*) AND dry season length

Identified experts and authors of review papers were consulted. Where appropriate, authors of papers were contacted to request data.

3.2 Study inclusion criteria

- **Relevant subject(s):**

Seasonally dry tropical forest (pan-tropical)

- **Types of intervention:**

Disturbance (see Table 1 for list of relevant types)

- **Types of comparator:**

Undisturbed forest (mature forests that show no signs of anthropogenic or natural disturbance) varying described in the literature – including terms such as unlogged, mature, closed forest.

- **Types of outcome:**

Regeneration by seedlings, vegetative regrowth and species regeneration composition

- **Types of study:**

Studies where inventories of seedling regeneration and composition had been taken on control (no disturbance) and experimentally disturbed forest (plot or stand level). Before and after study designs. Different lengths of dry season.

- **Potential reasons for heterogeneity:**

1. Age of seedlings/saplings
2. Age of sprouts
2. Basal area of overstorey prior to disturbance
3. Basal area of the overstorey after disturbance
4. Intensity of disturbance
5. Time elapsed since previous disturbance
6. Time elapsed between disturbance and assessment
7. Composition of overstorey
8. Soil type and geology
9. Herbivores

10. Climate (especially dry season length)
11. Ground vegetation

3.3 Study quality assessment

Articles were considered at full text and quality assessed by reviewers according to a hierarchy of evidence (Stevens and Milne (1997), Pullin and Knight (2003), (e.g. a randomised control trial was given more weight than a site comparison study) admitting or excluding them from the study. A minimum of 25% of the articles were considered by two of the reviewers and tested statistically to ensure agreement of quality was sufficiently high. Disagreement was resolved by a third reviewer.

3.4 Data extraction strategy

Data searches were conducted largely between August and October, 2008, with periodic checks for recent material throughout 2009. Study characteristics, design, quality, results and reasons for heterogeneity were extracted and recorded on specially designed data extraction forms. Attempts were made to collect primary data from authors where appropriate.

3.5 Data synthesis

A narrative thesis summarising the data was produced including study characteristics, design, quality, tabulated results and reasons for heterogeneity (Appendix 2). After consultation with a statistician, any data suitable for statistical analysis were analysed using appropriate techniques for the type of data extracted.

4. Results

The initial systematic literature identified in excess of 10,000 articles of potential relevance, indicating the poor specificity of the search terms. This was reduced to 534 on the basis of title by one reviewer (KM). Reviewers' comments on the draft protocol advised two additional search terms (drought and dry season length) which yielded a further 545 articles, of which 56 were duplicated in the initial list. Thus, 1023 articles were finally considered on the basis of title and abstract by one reviewer (MM). Of these, the full text of 35 articles was assessed (Appendix 1) by two reviewers (MM and KM) and 16 articles were retained for further analyses (Table 2). Agreement was substantial ($K=0.90$). Of these, 14 considered regeneration post-disturbance, and 2 considered facilitative effects of the forest canopy (Table 3).

Table 2. Regeneration composition by seedlings or sprouts (%). Where no seeding data given, percentage is of species resprouting in regrowth. The studies in bold are those with a forest/disturbance contrast. Others are post-disturbance regeneration or a chronosequence.

Study	Seed	Sprout	Disturbance	Time since disturbance	Rainfall
Ceccon et al. (2004)	80-86	35	Slash and burn	10-60 years	986
Dickinson et al. (2000)	84	16	Natural and felling gaps	4-11 years	1500
Gould et al. (2002)	89	11	Selective logging and burning	5 years	1110
Kammesheidt (1999)	14	76	Young fallow	2.5 years	1300
Kammesheidt (1999)	47	53	Older fallow	10-15 years	1300
Kammesheidt (1999)	80	20	Mature forest		1300
Kammesheidt (1999)	62	38	Fire-degraded stand	3 years	1300
Kennard et al. (2002)	40	60	High intensity burn	18 months	1129
Kennard et al. (2002)	10	90	Low intensity burn	18 monthys	1129
Kennard et al. (2002)	7	93	Plant removal	18 months	1129
Kennard et al. (2002)	0	100	Gap control	18 months	1129
Marod et al. 2002	25	75	Burned	20 months	1650
McLaren and McDonald (2003) FEM	20	80	Cut	14 months	780
Miller and Kauffman (1998) Biotropica	25	75	Slash and burn	15 months	750
Miller and Kauffman (1998) FEM		39	Slash and burn	15 months	750
Mizrahi et al. (1997)	71	29	Slash and burn	12 years	800-1000
Mizrahi et al. (1997)	46	54	Slash and burn	26 years	800-1000
Mostacedo et al. (in press)	55	45	Logging	18 months	1160
Otterstrom and Schwartz (2006)		45	Burned	3 years	1407
Sampaio et al. (1993)		94	Slash	6.5 months	803
Sampaio et al. (1993)		43	Low intensity burn	2 months	803
Sampaio et al. (1993)		21	Medium intensity burn	2 months	803
Sampaio et al. (1993)		10	High intensity burn	2 months	803
Vieira et al. JTE (2006)		77	Forest		1236
Vieira et al. JTE (2006)		59	Early succession	6 months	1236
Vieira et al. JTE (2006)		44	10 year old forest	10 years	1236
Vieira et al. JTE (2006)		52	25 year old forest	25 years	1236

Table 3. Evidence of facilitation – seedling survival (%) under forest canopy or in gaps

Study	Forest	Gap	Disturbance	Time since disturbance	Rainfall
McLaren and McDonald (2003) JTE	56	26	Cut	14 months	780
Vieira et al. Biotropica (2006)	56	51 (v. spp dependent)	Seedlings planted into gaps	12 months	1236

More detailed analyses were conducted on the 12 articles that included data for both seedlings and sprouts (Table 4).

Table 4. Data extracted from the reviewed literature and included in the analysis. Disturbance type (C - cut and B - burn); burn intensity (C - cut, CC – clear cut, S_B - slash and burn, HIB - high intensity burn, LIB - low intensity burn).

REGENERATION PATHWAY	COMPOSITION (%)	TOTAL (%)	DISTURBANCE TYPE	DISTURBANCE INTENSITY	TIME SINCE DISTURBANCE (YEARS)	RAINFALL (MM)
Seedling	20	100	C	C	1.2	780
Seedling	7	100	C	C	1.5	1129
Seedling	0	100	C	S_B	1.5	1129
Seedling	55	100	C	C	1.5	1160
Seedling	41	100	C	C	0.5	1236
Seedling	56	100	C	C	10.0	1236
Seedling	48	100	C	C	25.0	1236
Seedling	14	100	C	CC	2.5	1300
Seedling	47	100	C	CC	12.5	1300
Seedling	6	100	C	C	0.5	803
Seedling	25	100	B	S_B	1.25	750
Seedling	71	100	B	S_B	12	1000
Seedling	46	100	B	S_B	26	1000
Seedling	89	100	B	S_B	5	1110
Seedling	40	100	B	HIB	1.5	1129
Seedling	10	100	B	LIB	1.5	1129
Seedling	62	100	B	B	3	1300
Seedling	24	100	B	S_B	3	1407
Coppice	80	100	C	C	1.2	780
Coppice	93	100	C	C	1.5	1129
Coppice	100	100	C	S_B	1.5	1129
Coppice	45	100	C	C	1.5	1160
Coppice	59	100	C	C	0.5	1236
Coppice	44	100	C	C	10.0	1236
Coppice	52	100	C	C	25.0	1236
Coppice	76	100	C	CC	2.5	1300
Coppice	53	100	C	CC	12.5	1300
Coppice	94	100	C	C	0.5	803
Coppice	75	100	B	S_B	1.25	750
Coppice	29	100	B	S_B	12	1000
Coppice	54	100	B	S_B	26	1000
Coppice	11	100	B	S_B	5	1110
Coppice	60	100	B	HIB	1.5	1129
Coppice	90	100	B	LIB	1.5	1129
Coppice	38	100	B	B	3	1300
Coppice	45	100	B	S_B	3	1407

All statistical analyses were carried out using Genstat Release 8.0 (VSN international, Hemel, Hampstead, UK) statistical software. The data selected for the analysis were taken from Table 3. Where a range of values was reported for either rainfall, or the time since disturbance, the largest value was used. Also, where only the percentage contribution was reported for either seedlings/seedlings or coppice, then the unknown contribution was calculated using: unknown contribution = 100% - known contribution. Studies with any discrepancies in the reported values that could not be verified by the published manuscript were not included in the analysis. It was difficult to differentiate between burning intensity (as this cannot be quantified), therefore all studies that reported on the impacts of cutting and burning were lumped together for the analysis. Table 4 shows the data that was derived from Table 2, and used in the final analysis.

The analyses were conducted using a quasi-likelihood Generalized linear model with a binomial distribution and a logit link. A quasi-likelihood GLM was chosen to account for over-dispersion of the data and the binomial distribution with a logit link was chosen because the data analyzed represented a percentage or proportion of the regenerating vegetation. While a normal distribution with a log link could also be used, it was necessary to ensure that the predicted response did not exceed 100%. Therefore, a binomial distribution allowed for the analysis of regeneration composition as a proportion/percentage and restricted the predicted response between 0% - 100%. We assessed the impacts of rainfall (mm) and the time since cutting or burning (years) on regeneration composition (coppice vs seedlings), following cutting, cutting and burning, both cutting, and cutting and burning, with stems and roots remaining in place. We also assessed the interaction between the independent variates (rainfall or time since burning) and factors (regeneration composition) following disturbance. The response variate used for the analysis was the percent of regeneration accounted by either seedlings or coppice shoots. The binomial distribution requires that a "total" value is included in the analysis which is used to calculate the proportion. The total used for this analysis is 100% (100% in all cases, therefore if regeneration by seedlings account for 80% the total is given as 100%, giving a proportion of 0.8).

Rainfall and the time since disturbance had a significant effect on regeneration composition following cutting (Table 5). The observed trend was that, as rainfall increased, the proportion of regeneration accounted by seedlings increased, while the proportion of coppicing individuals decreased (Figure 2a) following cutting. On average, the contribution of coppice shoots was significantly larger than the percentage contribution of seedlings (post-hoc T- test; $P = 0.027$) regardless of total annual rainfall. However, an equal contribution by seedlings and shoots to regeneration following cutting is expected to occur at sites with a total annual rainfall of 1400 mm or more (Figure 2a). Similarly, as the time since disturbance increased, the proportion of regeneration accounted by seedlings increased significantly, while the percentage contribution of coppice shoots declined (Figure 2b). Again, on average, the percent contribution of coppice shoots far exceeded the contribution from seedlings over time (post-hoc T-test: $P = 0.001$), and an equal contribution by seedlings and shoots is expected to occur at approximately 19 - 20 years following cutting (Figure 2b).

Rainfall and the time since disturbance did not have a significant effect on regeneration composition following cutting and burning (Table 5). However, the overall trend was similar to that shown by regeneration following cutting. If cutting was followed immediately by burning, then as rainfall or the time since disturbance increases, the proportion of regeneration accounted by seedlings increased, while the proportion of coppicing individuals decreased (Figure 2b and c). On average, the contribution of coppice shoots was not significantly higher than seedlings, following cutting and burning when both rainfall and time since disturbance was considered. Burning, on average reduced the predicted time at which the contribution from both seedlings and coppice will be equal (7 - 10 yrs), and the total annual rainfall at which this will occur (approximately 1150 mm/year).

Overall, if the method of disturbance was not considered, total annual rainfall and the time since disturbance had a significant effect on regeneration composition (Table 5). The trend is similar to what has been reported so far. As rainfall and the time since disturbance increased, the percentage of regeneration accounted by seedlings increased, while the proportion of coppicing individuals decreased (Figure 2e and f). Also, overall, on average, the contribution of coppice shoots was significantly higher, irrespective of the time since disturbance and the total annual rainfall (pot hoc t-test; $P = 0.004$ and 0.039 for time since disturbance and rainfall respectively). The predicted time and total annual rainfall, at which the contributions will be similar, are between 16 - 18 years, and 1350 - 1450 mm/year.

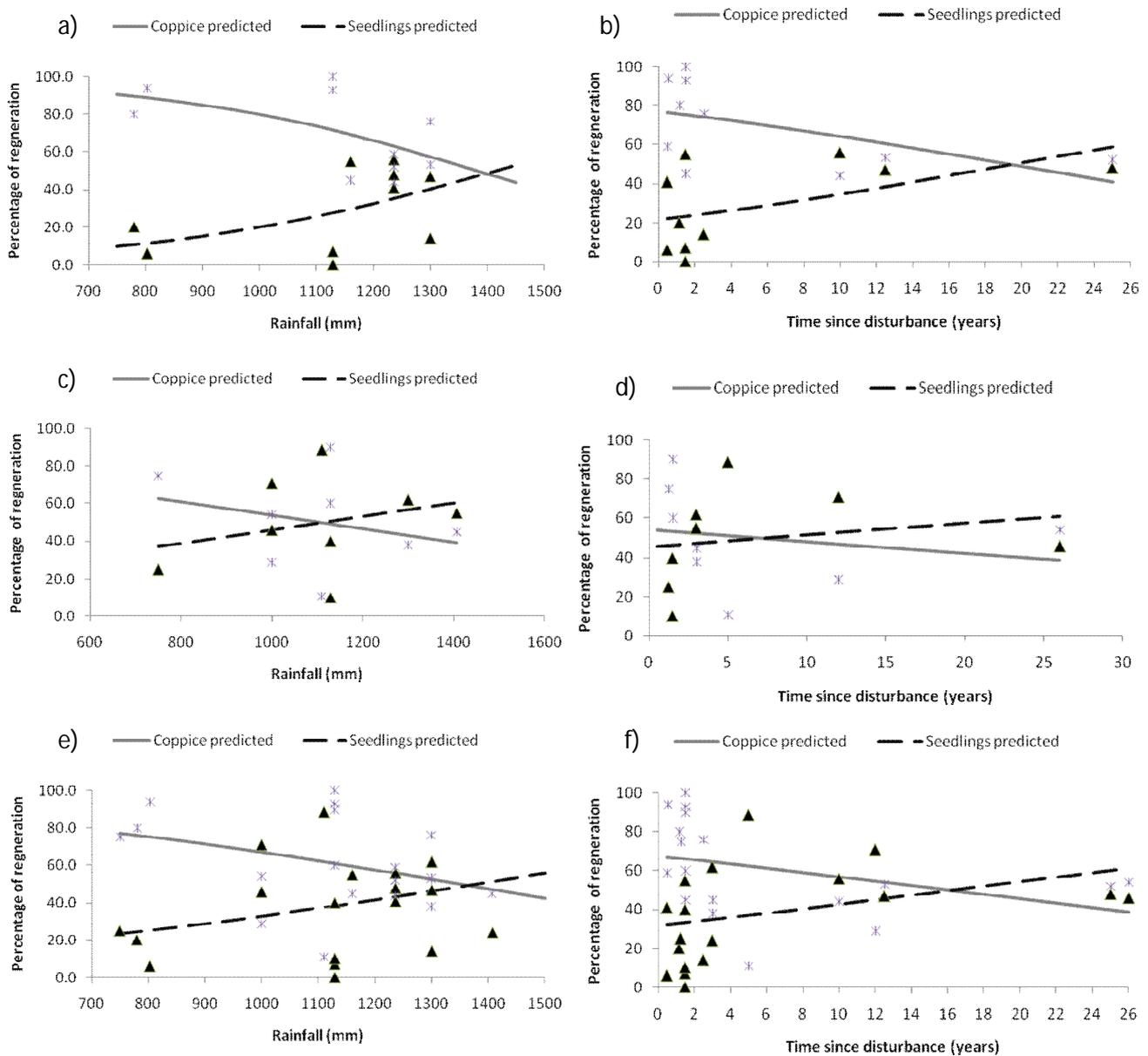


Figure 2. The effects of increasing rainfall and the time since disturbance on regeneration composition following disturbance by cutting (a - b) with stem and roots remaining in place, cutting then burning (c - d) with stem and roots remaining in place and irrespective of the type of disturbance (e - f; cutting and/or cutting then burning). The asterisk represents the observed proportion of coppicing individuals and the solid triangle represents the observed proportion of seedlings.

Table 5. Results of the quasi-likelihood generalized linear regression with a binomial distribution and a logit link. The model fitted includes the type of disturbance being assessed (Cut, Cut and Burn and both Cut and Cut and Burn), the independent variables rainfall (mm) (denoted 'Rain') or the time since disturbance (denoted 'TSD') and the factor 'Regen' which has two levels: regeneration by coppice (denoted 'Cop') and regeneration by seedlings. The response variate used was the percentage contribution of coppice or seedlings to the regeneration composition (Seedlings/Coppice regen.). The P-values and the model equations are also given.

Model fitted	P	Model Equations
<u>Cut</u> <i>Rain*Regen</i>	0.004	logit(Seedling regen) = Rain*0.00336 – 4.75 logit(Coppice regen)= Rain*0.00336 + Cop*9.82+ Rain.Cop*-0.00703 - 4.75
<u>Cut</u> <i>TSD*Regen</i>	0.005	logit (Seedling regen) = TSD*0.0663 - 1.292 logit (Coppice regen) = TSD*0.0663 + Cop*2.512+TSD.Cop*-0.1294 - 1.292
<u>Cut and Burn</u> <i>Rain*Regen</i>	0.818	logit(Seedling regen) = Rain*0.00336 – 4.75 logit(Coppice regen)= Rain*0.00336 + Cop*9.82+ Rain.Cop*-0.00703 - 4.75
<u>Cut and Burn</u> <i>TSD*Regen</i>	0.929	logit (Seedling regen) = TSD*0.0663 - 1.292 logit (Coppice regen) = TSD*0.0663 + Cop*2.512+TSD.Cop*-0.1294 - 1.292
<u>Cut and Cut and Burn</u> <i>Rain*Regen</i>	0.033	logit(Seedling regen) = Rain*0.00189 – 2.6 logit(Coppice regen)= Rain*0.00189 + Cop*5.32+ Rain.Cop*-0.0039 - 2.6
<u>Cut and Cut and Burn</u> <i>TSD*Regen</i>	0.027	logit(Seedling regen) = Rain*0.0472 – 0.768 logit(Coppice regen)= Rain*0.0472 + Cop*1.502+ Rain.Cop*-0.0928 - 0.768

5. Discussion

Coppicing is the primary pathway of regeneration following disturbance (cutting), with stems and roots remaining in place, in a dry tropical forest (Ewel, 1977; Murphy and Lugo 1986; Murphy et al., 1995; McLaren and McDonald, 2003b). The results suggest that regardless of the method of disturbance (cutting or cutting and burning), the period of time that had passed following disturbance, or the total annual rainfall of the dry forest sites, on average, the contribution of coppice shoots to regeneration following disturbance was significantly greater (if stems and roots remain in place). This is partially because stumps are less susceptible to rotting in the dry tropics (Ewel, 1980), and due to the lower probability of successful regeneration by seedlings (Ky-Dembele et al., 2007; McLaren and McDonald, 2003c; Vieira et al., 2006; Vieira and Scariot, 2006). The latter can be used to explain the significantly lower contribution by seedlings.

The regeneration cycle in the dry tropics is inexorably linked to moisture availability. This is important because there is a strong possibility that a recruited seedling will be left stranded in a drying soil (Ewel, 1980). While wet season conditions will allow for successful establishment of seedlings in the open or under the shade, high light conditions found in the open, un-shaded sites will exacerbate low moisture conditions during the dry season and lead to higher mortality (e.g. Gerhardt, 1996a; McLaren and McDonald, 2003a). Therefore, any anthropogenic activity that results in the opening

of the canopy will have a detrimental effect on seedling survivorship. Furthermore, while shading under the canopy may offer a facilitative reprieve, competition for moisture with other seedlings (as seedling densities tend to be higher under the shade in the dry tropics) and adult trees is intense, and will lead to mortality despite the advantages of the shade (McLaren and McDonald, 2003a). Therefore, trees in the dry tropics are more prone to reproduce vegetatively following disturbance (Ewel, 1980).

While the above is true for dry forest ecosystems, it is expected that as rainfall seasonality decreases, and the total quantity of rainfall increases, the probability of successful regeneration by seeds should increase, thereby increasing the contribution of seedlings to regeneration following disturbance. Artificially maintaining high moisture levels during the dry season will increase seedling survivorship significantly (e.g. Blain and Kellman, 1991; McLaren and McDonald, 2003b). Also, seedling survivorship in the dry tropics is most correlated to the moisture conserving status of the habitat (e.g. Hammond, 1995). Thus, it is expected that moisture stress will be less in dry forest sites with a higher total annual rainfall, and the probability of successful regeneration by seedlings in these forest will be higher. Also, cut stumps will be more susceptible to rotting; therefore this will reduce the contribution of coppice shoots. Our analysis appears to support this, as the studies that were conducted in dry forest sites with an above average annual rainfall, recorded a significantly larger contribution by seedlings to regeneration following cutting. The threshold total annual rainfall, as evident from Figure 1a, appears to be approximately 1400 mm/year and greater. It is at this point that the contribution from both seedlings and coppice is predicted to be near equal. This however, will need to be fine tuned by including additional studies from dry forest ecosystem as they become available.

Interestingly, the analysis also points to the fact that coppicing individuals initially dominate the regenerating vegetation. This advantage is lost after approximately 20 years, after which, seedlings will then start to dominate the regenerating vegetation. A possible explanation for this maybe that, while dry tropical forests do show a very high resilience, that is, they have the ability to recover the structure and diversity lost very quickly, coppice stumps will never attain the same height, DBH or canopy cover of the pre-disturbed forest. A direct consequence of coppicing following cutting with stems and roots remaining in place is a very patchy development of a long-lived stage characterized by large densities of very small trees (Ewel ,1977; Murphy and Lugo, 1986; Murphy et al., 1995). This will allow for more resources to be available to recruited seedlings. Also, the shade provided by re-grown coppice stumps may be enough to ameliorate prevailing conditions, providing ideal conditions for seedling establishment.

Furthermore, if the cause of disturbance is not taken into account, the contribution of the regenerating vegetation shows a similar trend; the contribution of coppice shoots to the regenerating vegetation decreases over time and with an increase in annual rainfall. The non-significant results for burning may have been due to the wide variation in the intensity of burning. The intensity of burning is difficult to determine, as such, we lumped high and low intensity burns together. Also, burning will have a differential effect (unless the community in question is fire adapted) and might favour only a few species. Thus, the ability to regenerate after cutting and burning may be more dependent on the intensity of the burn and the ability of seedlings or stumps to withstand burning.

An aspect of dry forest regeneration not considered with the search terms used was the effect of fragmentation on tropical dry forest regeneration in relation to propagule availability for regeneration. It can be plausibly assumed that fragmentation may have less of an effect on tropical dry forests than moist forests due to modes of seed dispersal. In moist forests, vertebrates are the main agents of seed dispersal with wind dispersal only occurring for 0 – 16% of species whereas wind dispersal is found in 30 – 63% of canopy tree species in dry forests of Bolivia, Brazil and Costa Rica (Vieira & Scariot, 2006). In addition, the very nature of the anthropogenic landscapes where dry forests are found means that there are often populations of large herbivores such as cattle which can also be effective seed dispersers, particularly for leguminous trees and shrubs (Ferguson et al., 2003, Chazdon et al., 2009). Further review of regeneration mechanisms should incorporate these important facets.

No evidence of facilitation was apparent in the studies reviewed; experimental studies will be required to establish if there are any effects in dry forest regeneration. Quesada et al. (2009) in a review of succession and management of tropical dry forests in the Americas have as one of their conclusions, that “we should identify the main parameters involved in tropical dry forest succession to develop models of recruitment dynamics in key dry forest plant species that facilitate the process of succession following natural or human-induced disturbances”.

6. Reviewers’ conclusions

6.1 Implications for management/policy/practice

The driver for this review was to better understand the factors which influence tropical dry forest regeneration, with a view to identify conservation actions for such forests. The results would seem to confirm that these are vulnerable ecosystems, highly dependent on vegetative regeneration in the short term. This will restrict genetic diversity, and limit the forests’ ability to spread their range in a changing climate. It suggests that the current observed fragmentation of dry forests in anthropogenic landscapes can maintain themselves without increasing threats, but limited in their ability to increase fragment size. Given their high biodiversity and limited range for expansion, they should clearly be accorded high conservation priority. Restoration efforts should consider the most effective means of vegetative propagation, particularly in areas of highest human activities which should be given priority status. Such restoration efforts should aim to increase connectivity between previously disturbed fragments which show reasonable successional development and hence recovery of biodiversity.

6.2 Implications for research

From a research perspective, result such as these could be used to develop more generic models of dry forest regeneration patterns which will enhance our ability to restore these threatened ecosystems. We need more climate change and regeneration studies in dry forest ecosystems, so that a comprehensive theory and explanation of dry forest dynamics can be built to afford greater understanding of the process and mechanisms governing regeneration in the dry tropics, this has been largely achieved

for temperate and tropical rainforest ecosystems, but is as yet under-developed for tropical dry forests.

7. Potential Conflicts of Interest and Sources of Support

No conflicts of interest to be declared. This systematic review is funded by Bangor University and the University of the West Indies, Jamaica.

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Appendix 2. Characteristics of included studies

Study	Location and Climate	Experimental Design	Intervention and comparators	Outcomes measured	Summary of results	Sources of heterogeneity	Include in analysis (why)?
Albuquerque (1999)	Northeast Brazil Rainfall 567 mm annually	3 steer stocking rates (heavy, moderate, light) combined with 2 grazing systems (continuous, rotational (3 sub-divisions)) and an ungrazed control conducted over 6 years. In a second phase (three years long) all grazing treatments became continuous. Not replicated but 'plots' were 40 – 80 ha. 6 20 x 5m plots in the continuous grazing and control, and 12 in the rotational plots (4 in each division)	Grazed v. ungrazed	Frequency of herbaceous species and densities of seedlings (<0.5m) of woody plants annually using 5 2 x 0.5m quadrats Mortality and growth in canopy cover of 7 selected species measured biennially Density of trees and shrubs (>0.5m) by PCQ	Stocking or grazing did not affect frequency of herbs which were less abundant in eth control (woody spp competition) Herbs increased in frequency with increased rainfall Increased sticking rate increased mortality and decreased growth in woody shrubs	Ecological characteristics: Shrubby caatinga Methodology: No replication	No – only useable data is seedling density
Ceccon et al. (2004)	Yucatan, Mexico Rainfall 986 mm Dry season December – May	16, 12-m x 12-m plots within secondary forests at two sites 1) abandoned 60 yrs ago and 2) abandoned 10 years ago. Four treatments: 1) control, added N, added P, added N and P). Four replicates randomly allocated in the 16 plots per site. Duration 24 months	Sites were previously used for slash and burn agriculture. Fertilizers added twice per yr N (220 kg/ha/yr) and P (75 kg/ha/yr). N and P concentrations between forests 1.30% and 1.34 %; 0.22 and 0.34% in the young and old respectively before	Final species richness Number of individuals Diversity Seedling survival Total number of new recruits Species origin (seed or sprout)	Recruitment was highly seasonal and reached a peak during the rainy season. 35% of species showed an ability to regenerate by sprouting 80% and 86% in the young and old forest (respectively) regenerated by seed. After 24 months total percentage	Methodology: Light measured only once, and therefore no account of seasonal variability in light due to leaf fall/deciduousness during the dry season.	Yes – Impact of rainfall on seedling mortality, and seedling vs sprouting as a regenerative mechanism

			<p>the experiment. Seedling dynamics (within the 6 m² of each plot, four subplots 1 m² each), stem height ≤ 1 m tagged and recorded. 64 permanent subplots Light conditions Bulk density</p>		<p>mortality of recruited seedlings were 63% and 54% for young and old forest respectively. Mortality was the lowest during the first half of the rainy season. The survival time of seedlings regenerated by spout is much higher than from seeds in the secondary forest.</p>		
Dickinson et al. (2000)	<p>Quintana Roo, Mexico</p> <p>Rainfall 1500 mm dry season (with <100 mm rainfall per month) runs from January through April</p>	<p>Stratified-randomly selected natural gaps, felling gaps, and closed-canopy sites were sampled (only gaps estimated to be 20 m² or greater). Used a 15 km long logging road, randomly located points along this road and at each point established a single 500-m long transect perpendicular to the road. The side of the road was randomly determined. A single closed-canopy site, natural gap and felling gap were then sampled. Additionally all large natural (>100 m²) and felling gaps (>150 m²) encountered were sampled.</p>	<p>4 – 11 year old natural and felling gaps. All stems ≤ 5 cm DBH were sampled in sets of 10 m² plots in closed canopy and gaps. Five adjacent plots were sampled in each closed canopy site. In most gaps, as many adjacent plots were sampled as would fit. In largest gaps, 6 – 12 adjacent plots were sampled in a randomly chosen portion of the gap. Origins of the 10 tallest stems > 1.5 m in height within the entire area of the canopy gap were determined (seedlings or sprouts).</p>	<p>Stems > 5cm enumerated Heights of the 10 stems > 1.5 m in height</p>	<p>Logging promoted root sprouting. Advance growth accounted for a higher proportion of tall stems in natural than felling gaps. The proportion of tall stems that originated from seeds or small seedlings at the time of gap formation was higher in felling than natural gaps and increased with canopy openness only in felling gaps.</p>	<p>Methodology: Not really a stratified random approach? The number of plots used in each gap. The distances between the plots. Does each plot within each gap represent an independent sample if as many adjacent plots that could be fitted were used (pseudo-replication)? How was the 10m² square plot derived ? Species classification not necessarily based on empirical evidence. Time period after gap creation.</p>	<p>Yes – sprouting vs seedling after gap creation</p>

			Canopy openness was measured in the centre with a spherical densiometer Species classification				
Gould et al. (2002)	S.E. Bolivia Two sites: Rainfall 1110 mm (6-7 month dry season) and 1542 mm (4 month dry season)	Transect through burnt and unburnt areas. At 100-m intervals, secondary transects established perpendicular to the primary transect. Sample locations 50-m intervals along the secondary transect. 9 x 9 m ² plots established at each interval. 12 and 13 species of trees sampled at each site respectively in 15 – 18 plots per-treatment at each site.	Burning 5 yrs before the study Light selective logging in the dry forest in the 70's and 80's Dry vs humid sites Burnt vs unburnt Seedling vs sprouts > 20-cm tall with basal diameter ≤ 5-cm Seedling and sprouts < 20 cm tall counted and identified in two 1 x 1 m ² plots in the centre of each 9 x 9 m plots.	Abundance (number of regenerating stem) Percentage of regeneration (sprouts and seedlings)	Tree regeneration was more abundant in the dry forest than in the wet Resprouts were less abundant than seedlings Burning favoured the abundance of some species Resprouts were larger than seedlings in burnt and unburnt plots	Ecological characteristics: Very light logging. Size and species limits for samples Methodology: Period elapsed after cutting and burning.	Maybe – the time of sampling after cutting and burning may not be comparable to say sampling right after cutting and burning. Cutting occurred long before sampling and at very low intensity.
Heuberger et al. 2002	Bolivia Rainfall 1130 mm 6 month dry season	40 logging gaps ranging in size from 240 m ² to 840 m ² were assigned at random to one of 3 treatments or a control 1) mechanical cleaning (using machetes and chainsaws) of all competing vegetation 2) Mechanical cleaning followed by prescribed burning 3) Prescribed burning without mechanical cleaning 4) control	One month and 8 months following burning: all commercial tree species seedlings and saplings (trees ≤ 3-m tall) tagged and height measured Non-commercial plants > 2 m counted and percent cover in each quadrat	Relative height growth rates of commercials Count and percent cover of non commercials	Density and relative height growth of total commercial regeneration did not differ among treatments	Methodology: Short duration of the experiment, only commercial species included. Additional data on resprouting would have been helpful	No – looked at a specific set of seedling and on seedling growth. Impacts of cutting on burning on seedling vs vegetative regrowth not addressed

		Replicated 10 times Duration 8 months 2, 2-m wide transects established in all 40 gaps along the long axis of the gap 4m ² quadrats established at 2 m intervals along the transect used to assess seedling densities					
Kammesheidt (1999)	Paraguay and Venezuela Paraguay: Rainfall 1300 mm dry season, with a monthly precipitation of < 60 mm, lasts from May to August Venezuela; Rainfall: 1750 mm with a dry season from December to March	8 circular plots 500-m ² each, randomly established in 1) younger forest fallows (2, 3, 4 and 5 year old), 2) older forest fallows (10 and 15 year old), 3) fire-degraded stand (stratified random design with 4 plots in both slight and severely damaged areas respectively) and 4) mature forest. Sampling units: 8 plots of 2-m x 2-m 3 stands logged 5, 8, and 19 years. 30 circular plots 400 m ² , located in each stand 25 plots established in unlogged stands 2 x 2 m plots nested within each sampling unit	Paraguay: Seed established individuals vs above ground sprouts vs root suckers Venezuela; seed established vs vegetative regrowth (no distinction between sprouts and root suckers)	Abundance	Paraguay: Resprouts declined from 76% in the young forest fallows (2 -5 y old) to 48% and 14% respectively in older forest fallows (10 and 15 y old) and mature forest. Venezuela: Proportion of resprouts from young to old logged stands increased 10% to 16% to 17%. Root suckers more common than above ground sprouts. Regeneration by seed more common than vegetative regen in all sites combined.	Ecological characteristics: The Venezuela site is at the wetter end of the dry forest spectrum, and might be classified as a seasonal moist/humid forest. This maybe exemplified by the lower incidence of coppicing. Different pre-treatments between the sites farming and burning (Para) and logging (Ven). Different sampling regimes for both sites. Methodology: Un-balanced sampling design. Only individuals 30 – 130 mm tall were reported.	Yes: But only for Paraguay. Also the size of the individuals sampled is restricted. The different rainfall and sampling regimes and the different pre-treatments muddled the results.
Kennard (2002)	Bolivia Annual rainfall 1129 mm with a strong dry season from May to October	14 fallows representing 12 different ages from 1 to 50 y. 1 replicate of each age (except 1 y which had 3) 6 50m x 20m plots in	Different fallow ages v. mature forest	Tree species richness Total plant cover <2m tall and > 2m tall by life form (graminoids, herbs, ground bromeliads,	Tree species richness, canopy cover and basal area reached or surpassed 75% of mature forest levels in the 5-, 8- and 23-yo	Methodology: No replication	Maybe – change in species composition (IV)? Results are potentially attributed to a high percentage

		each fallow with smaller nested quadrats within		shrubs, vines and trees	stands. Stem density of the 50-yr stand twice that of mature forest		of sprouting trees, but data not given. Contact author?
Kennard et al. (2002)	Bolivia Rainfall 1129mm with a strong dry season from May to October	16 recently felled gaps 1, 20 x 20-m block divided into 4, 10 x 10 m plots, 2, 2 x 2-m subplots near the centre of gap and 2 near the edge. Duration: 18 months	One of 4 treatments randomly assigned to each 10 x 10-m: 1) high-intensity burn; 2) low-intensity burn; 3) above ground plant and coarse debris removal; 4) a harvested gap control.	Seedling and sprout density and mortality Seedling and sprout size (height, crown area, and basal diameters)	Overall tree seedlings were more abundant than tree sprouts. Few differences in seedling density among treatments. Sprouts were most common in plant removal and low-intensity burn treatments. Seedling mortality was higher than sprout mortality during the first year after treatments. Sprouts were taller, had more stems per individual, larger crown areas and larger basal diameters than seedlings. After 18 months 85% of individuals > 2.5 m tall were sprouts with most seedlings > 2.5 m tall were found in high intensity burn treatments where sprouts were less dominant.	Methodology: Block and plot layout	Yes
Lebrija-Trejos et al. (2008)	Oaxaca, Mexico Rainfall 900 mm with 90% falling between late-May to	15 sites with fallow periods of 1, 3, 5, 7, 10, 12, 14, 18, 22, 27, 32, 37 and 40 yr and a mature forest site.	Fallow periods	Diversity Canopy height Plant density Crown Cover	Shrub phase characterized early succession (0 – 3 years). Canopy height, plant		Yes

	mid-October	At each site, 30 x 30 m plots established. 4, 20 x 5-m transects with 2-m corridor within each plot. Each transect divided into four 5 x 5-m quadrats			density, and crown cover stabilized in less than 15 yrs, whereas species richness, diversity and basal area continued to increase. Pioneer species group has very low diversity and the long-lived pioneer phase typical of humid forests is absent.		
Marod et al. 2002	Thailand Annual rainfall normally exceeds 1650 mm and mainly falls from May to October.	4 ha PSP (200 x 200 m) 1 ha plot within for seedling dynamics (1.5 x 1.5-m quadrat with 10 m distance between each one.	Area burnt 1 year before All individuals < 1.3 m high Rainfall and soil water tension (for 2 years) Hemispherical canopy photographs (twice, rainy and dry season for one year)	Seedling mortality Survival rate	Mortality higher for the first year seedlings gradually decreases for older ones. Most cohorts showed a pattern of high emergence from the end of the dry season to the beginning of the rainy season and high mortality during the dry season. Mean survival rate for all seedling species was quite low and differences were recorded for wet and dry seasons.		Yes
Martini (2008)	Brazil Rainfall 1400mm annually. Dry season (April-September) mean monthly rainfall <60mm. Extended	Permanent plot 10.24ha – 320 x 320m divided into 256 sub-plots of 20 x 20m All disturbance events to trees with basal diameter >20cm	Degree of disturbance	Disturbance mode and basal diameter, age class, dead or alive, presence of resprouts	High proportion of resprouting observed and species with best resprouting ability were most abundant		No – no forest control

	dry periods common.	<p>counted.</p> <p>Disturbance modes were (i) Uprooted: entire trees that had fallen exposing their roots. (ii) snapped – entire trees that had their trunks broken at any height; (iii) standing – entire trees that had died while standing or trees that had lost the largest portion of their crowns; (iv) inclined – entire trees, dead or alive, that had inclined to a steep angle at which crown displacement created a canopy opening; (v) stem – the dead stem (>20 cm diameter) of a multi-stemmed tree; (vi) branch – the loss of part (>20 cm diameter) of the crown of a tree; (vii) complex – entire trees that could not be classified into the categories described above, usually because the same tree demonstrated two or more disturbance categories.</p> <p>Time since disturbance was classified into 3 age classes based on previous inventory data (old, intermediate,</p>					
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		recent)					
McLaren and McDonald (2003) FEM	Jamaica Rainfall c. 780 mm Small rainy season in May to June with the main rainy season occurring in October usually followed by a dry period, which is 4–5 months long from December to April	12, 15 x 15-m plots in a randomized block design with 4 blocks and 3 treatments per plot Duration 14 months	Treatments: 96% reduction in basal area vs 38% reduction vs no removal 10 of the largest shoots on all stumps	Height and DBH	Of the 51 species sampled 3 did not coppice. 81% of all individuals produced shoots. Diameter recovered was approximately 29% per year		Yes-But no comparison between origin of regeneration: shoots vs seeds
McLaren and McDonald (2003) JTE	Jamaica Rainfall c. 780 mm Small rainy season in May to June with the main rainy season occurring in October usually followed by a dry period, which is 4–5 months long from December to April	12, 15 x 15-m plots in a randomized block design with 4 blocks and 3 treatments per plot Treatments: 96% reduction in basal area vs 38% reduction vs no removal	Seedling dynamics in: Treatments: 96% reduction in basal area vs 38% reduction vs no removal	Light (PAR) Seedling dynamics : 1) mortality 2) survival, 3) growth (root collar diameter) and 4) recruitment	Recruitment was highly seasonal, with most species being recruited during the wet season. Mortality was highest during the dry season and conversely survival was highest during the wet season. Highest absolute growth occurred in the clear-cut plots. Highest seedling densities were recorded within the uncut and partially cut plots.		Yes
Miller (1999)	Jalisco, Mexico Rainfall 748 +/- 119 mm/yr, 80 percent of which occurs from July-October	8, 30 x 100 m plots 3 plots were slashed and burned 95 days later 2 plots were slashed and burned 80 days later 3 plots slashed and burned 65 days later Before burning: line	Cutting preburn vs post burn	The number of shoots Length of the longest shoot Growth Foliar crown area	88% of the individuals that coppiced during the interval between slashing and burning did not survive the initial slash burns. No significant difference in the number of shoots,	Methodology: Transect used within the plots to assess sprouting instead of assessing all cut stumps found within the plots. No mention of how many line transects, and the space between individual transects, so	Maybe-But no post and pre treatment comparison of structure. No real indication of the percentage of cut stumps that coppiced because of the method of

		transects used to assess sprouting with > 1 cm basal diameter Pasture slashed 11 yrs earlier and brunt 3 times			length of longest shoot and foliar crown area between woody individuals that coppiced before burning and those that coppiced after burning.	no indication of sampling intensity for each plot. Only stumps with coppice shoots were sampled.	assessment employed. Can only assess the impacts of burning on coppice survival and growth.
Miller and Kauffman (1998) Biotropica	Jalisco, Mexico Rainfall 748 +/- 119 mm/yr, 80 percent of which occurs from July-October	9, 30 x 100 m plots 3 plots were slashed and then burned, crops grown after which they were grazed	33 woody seedlings and 33 woody species sprouts/plot were identified and tagged along line transects within 3 of the 9 plots Mean crown area	Height and diameter of tallest stem Elliptical crown area Relative growth rate (for height, diameter of the tallest stem and crown area) Mortality	One year after initial measurements, 29 percent of the seedlings and 13 percent of the sprouts were dead. More shrub species contributed to seedling numbers, while more trees contributed to the number of sprouts. Each of the seedling means (number of stems/individual, height and diameter of the tallest stem, elliptical crown area) was significantly smaller than that of sprouts, at all measurement periods, but relative growth rates were similar. The presence of seedlings increased species diversity compared to calculated diversity excluding seedlings	Methodology: Transect used within the plots to assess sprouting instead of assessing all cut stumps found within the plots. No mention of how many line transects, and the space between individual transects, so no indication of sampling intensity for each plot. Only a fixed number of species assessed per plot so numbers per species vary which means that some were not properly replicated. Would be better to have fixed number of individuals per species as well.	Maybe – a fixed number of species
Miller and Kauffman (1998) FEM	Jalisco, Mexico Rainfall 748 +/- 119 mm/yr, 80 percent	9, 30 x 100 m plots All plots were slashed and then burnt, slashed and then burned, crops	Uncut forest vs after cutting/before burning and after burning vs a	Species abundance Species diversity Number of sprouting species	Slashing, burning and cultivation, and grazing thinned the forest through	Methodology: Unbalanced design, line transect was used to sample treatment plots	Maybe

	of which occurs from July-October	grown after which they were grazed. 10, 2 x 100-m belt transects established in uncut forest 6, 2 x 100-m transects in pasture Line transect used to sample treatment plots	pasture		mortality, altered relative abundance of species, and simplified the community by eliminating 29% of sprouting species encountered before burning		
Mostacedo et al. (2009)	Bolivia Rainfall 1160mm. 5 month dry season May - October	Stump sprouts: Site 1: Selectively logged 1 year before study. Stumps and stump sprouts of 6 species diameter and height recorded. Site 2: Logged 2 years before study. Stumps and stump sprouts of 10 species diameter and height recorded. Site 3: Logged 5 years before study. Stumps and stump sprouts of 6 species diameter and height recorded. Regeneration type: Densities and sizes of seedlings and sprouts <2m tall of 16 species in microsites logged 1.5 years previously. Logging gaps (n=16); logging roads (n=16); log landings (n=8); primary skid trails (n=16); secondary skid trails (n=16)	For stump sprouts: time since logging For regeneration type: Logged vs non-logged micro-sites	Seedling densities, root sprouts, stem sprouts	Number of sprouts declined with increasing stem diameter and stump height. Probability of sprouting varied between species. Light-demanding species regenerated more from seeds and root sprouts than stumps. Seedling densities were higher in logged microsites opened by logging while sprouts were equally common across microsites.	Ecological characteristics: Intensity of disturbance	Yes – for microsite evaluations
Murphy and	Puerto Rico	120 m x 120 m site	Mature forest	Taxonomic	>12,000 stems per		No seedling or

Lugo (1986)	Annual rainfall c.860mm with dry season January-March, but also moisture limitation during mid-late summer. Moisture availability highest August/September to December, but water deficits exhibited 10mo per year	divided into 144 10m x 10m sampling plots 15 control plots and 5 plots cut to ground level for biomass estimation	records only	composition and forest structure in control plots Biomass in cut plots	hectare. Of all stems >2.5 cm dbh, 57% are stump or root sprouts (cut 50 y previously). Dry season result sin 50% reduction in leaf area. Low tree species richness and community biomass relative to wetter forests.		sprout data
Negreros-Castillo and Hall (2000)	Quintana Roo, Mexico Rainfall 1000 – 1200 mm mostly in the period July-December	5, 0.5 ha plots. In each plot after cutting residual basal area were 100%, 92%, 72%, 65% and 45%. Duration 3 yrs	128, randomly chosen stumps residual basal area compared	Number of sprouts per stump Height Stump size	Sprouts varied from 1 to 6, sprout heights varied from 1.0 m to 5 m	Methodology: No replication	Maybe – No mention of the percentage of cut stumps producing shoots, restricted number of species and stumps assessed
Negreros-Castillo and Mize (1993)	Quintana Roo, Mexico Rainfall 1000 – 1200 mm mostly distributed August-April	5, 0.5 ha plots. In each plot after overstorey removal were 0%, 8%, 28%, 45% and 55% Each plot divided into 50, 100 m2 subplots, with a 2 m2 regeneration plot in the centre)	0%, 8%, 28%, 45% and 55%	Seedling count Seedling diversity	The regeneration population was similar in density and composition before overstorey removal	Methodology: No replication	Maybe – no growth info, no comparison with vegetative regrowth, etc.
Otterstrom and Schwartz (2006)	Nicaragua Mean annual precipitation c. 1500mm, dry season December - March	60 5x15m plots in upland forest arranged in 4 groups of 15 Pre-treatment (fire) measurements and i.d. of all woody species >1.5cm dbh. Species counts for all species <1.5cm dbh Experimental burns in	Comparison of burned v. unburned plots	Identification of all woody species >1.5cm dbh. Species counts for all species <1.5cm dbh Post-fire mortality and presence and type of sprouting behaviour (basal, root or stem);	Recovery between species –classified as either resistant, resprouters or recruiters	Methodology: Lack of spatial independence	Yes – differential species response?

		<p>¾ of plots</p> <p>Pre-fire measurement repeated 1, 2 and 3 y post-burn</p>		<p>(percent survivorship, frequency of sprouting, number of sprouts per individual and type of sprouts</p> <p>In 15 most abundant sapling species – fire injury assessed</p> <p>Post fire changes in seedling density</p>			
Perkulis et al. (1997)	<p>Yucatan, Mexico</p> <p>800-1000mm annual rainfall. Dry season October - June</p>	<p>2 abandoned patches of deciduous forest of different age 10 and 26 y-o)</p> <p>5 10 x 20m contiguous plots at each site - inventory of all woody plants >1cm dbh and coppice shoot v. seed origin recorded</p> <p>1 4 x 4 m sub-plot for all woody stems < 1cm dbh and in the subplot a further 1 x 1 m subplot for the herbaceous seedling layer</p>	<p>2 abandoned patches of different age 10 and 26 y-o)</p>	<p>Inventory of all woody plants >1cm dbh and saplings < 1cm dbh</p> <p>Coppice shoot v. seed origin recorded</p> <p>Species densities</p> <p>Similarity indices</p>	<p>30 and 50% of individuals regenerated from coppiced shoots in the 12 and 26 y-o stands respectively</p> <p>Stands were similar in composition</p> <p>Few late successional species present in older stand (lack of seed source and perturbation)</p>	<p>Ecological characteristics: Young secondary forests</p>	<p>Sprouting data – but no undisturbed forest comparator</p>
Read and Lawrence (2003)	<p>Yucatan, Mexico</p> <p>Precipitation gradient from c.900 – 1400 mm annual rainfall 3mo – 6mo dry season associated</p>	<p>Three study regions along a precipitation gradient</p> <p>Within each region 10-13 500m² circular plots in secondary forest (2-25 y since abandonment) to mature forest</p>	<p>Secondary v. mature forest and precipitation regimes</p>	<p>Stems > 1cm dbh AGB, wood density and tree height</p>	<p>Within 12-25 y biomass reached half of mature forest levels. Recovery to pre-logged state estimated at 65-120 y. Biomass is profoundly affected by forest age, and less so by annual precipitation.</p>		<p>No – tree data only</p>

					Variability in forest structure depends more on differences in water availability and recent human disturbance.		
Rico-Gray and Garcia-Franco (1992)	Yucatan, Mexico 900-1000mm annual rainfall. Dry season winter and early spring and wet season between June and October	Forest patches – slashed and burned and 1, 6, 10, 15, 30, 40 and 100 y-o sites. Patches varied from 2-8 ha depending on age. Records from contiguous 10 x 10 m plots in 2 rows of 5 Traces of coppicing ‘recognised’	Different ages of secondary forest	Inventory (abundance) of all woody plants \geq 1cm dbh Species diversity Similarity indices for sites Soil seed bank	Species diversity similar between sites One third of stems originated from coppice shoots Original forest species rare or absent in 1-20 y-o forests	Ecological characteristics: Intensity of burn Methodology: Not clear how coppicing was recorded No replication	Yes – species diversity, even though comparator is older secondary forest. Might be possible to get primary forest data – a Miranda (1958) study is referred to Coppice stems not presented as separate data – would have to contact authors
Sabogal (1992)	Nicaragua Rainfall c. 1500mm annually in the undisturbed area and 1700mm (5 month dry season <50mm) in the secondary area	‘Undisturbed’ forest: 120 plots 50 x 20m, distributed over 1000ha. Regenerating stems (2.5 – 9.9 cm dbh) recorded in 2 randomly selected subplots 10 x 10m. Young trees and saplings (dbh <2.5cm and >50cm height) recorded in 8 transects with 25 2 x 2m squares placed in 8 randomly selected plots Secondary forest: 69	Undisturbed v. secondary forest	All trees >10cm dbh species, dbh, stem quality and crown position recorded	Major species inventory. Stand characteristics. Density of regenerating species in the undisturbed forest	Ecological characteristics: Intensity of disturbance Climatic/edaphic differences between sites Methodology: Aggregate data presented so no replication	No – no seedling data for the secondary forest

		plots of 0.09 ha in a 6.2ha study area. No seedling plots					
Sagar and Singh (2005)	Northern India 850 – 1300 mm annual rainfall, 86% during June-August monsoon	Five forest sites representing a disturbance gradient. 3 x 1ha contiguous plots at each site – divided into 100 10 x 10m quadrats. In the centre of each quadrat, a 2 x 2 m plot for seedlings (<3.2 cm diameter but >= 30 cm height) and saplings (3.2 to < 9.6 cm dbh). Seedlings < 30 cm height considered ephemeral and not counted	Intensity of disturbance between plots – unclear if the least disturbed plot represented undisturbed forest	Stem diameters and species recorded – separated into size classes	Sites were different in terms of seedling composition, and seedling and adult distributions were not spatially associated	Ecological characteristics: Size of seedlings/saplings – Intensity of disturbance	Yes – species diversity
Saha and Howe (2003)	Central India 1400 mm annual rainfall during June to October monsoons. Severe dry season December - May	24 3x 3 m plots established in a 4 ha Mendha forest. 12 plots burned, 12 protected	Burned v. unburned forest plots	Seedlings (<1 y-o) and juveniles (>1 y-o), <1.5m height) marked and identified to genus 12 months post-burning Root-sprouters and root-crown-resprouters distinguished	30% decrease in seedling diversity in burned plots Fire-related mortality of seedlings was 74% for 17 root-crown resprouters, compared to 63% for six root-sprouters	Ecological characteristics: Previous fire history (low intensity, anthropogenic) Fire intensity	Yes – may need to aggregate root-sprout and root-crown-resprout data in the absence of any other data from different studies
Sampaio et al. (1993)	Brazil 803mm annual rainfall, dry period May- November	Caatinga forest Six plots, 0.24ha each. 2 plots burned at each of three intervals. Separated by firelines serving as unburned controls Measurements collected in belt transects 1m wide in	Burned plots v. cut and unburned plots	Number of coppicing and non-coppicing stumps with a stem diameter >1cm at soil surface recorded Densities of sprout species recorded and relative abundance	>94% stems coppiced after slashing. Burning reduced number of plants coppicing and coppice crown area, depending on severity of burn Species displayed	Ecological characteristics: Severity of burn	Maybe – would have to assume cut and unburned areas (longitudinally?) as forest comparators

		each treatment (number of transects varied between treatment)		Sprout survival Crown area of each coppicing plant (ground cover)	variable coppicing response to burning. Some increased coppicing with fire severity.		
Sussman and Rakotozafy (1994)	Southwest Madagascar Annual rainfall 750mm, 600mm precipitation Nov-March	Gallery forest dominated by <i>Tamarus indica</i> protected (for the last 20 years) and grazed 25 transects of 50m x 2m. All adult individuals (>2.5cm) recorded. In protected area, 10 transects near river, 10 farm from river (different communities) and 10 in unprotected forest 25 seedling plots or 2m x 2m selected (one per transect).	Protected v. grazed forest	Diversity and proportion of native and exotic species Number of individuals of most common species Species and number of individuals <2.5 cm diameter in seedling plots either 'open' or 'covered' (but data not presented separately)	No noticeable differences in density, diversity, size classes, or proportion of native species between protected and unprotected areas	Methodology: No replication	Yes – seedling data only. Difficult to interpret whether adult data relate to disturbance in the absence of growth rates
Tálamó and Caziani (2003)	Argentine Chaco 700mm average annual rainfall – 80% precipitation October - March	Chaco forest 2m x 100m plots 12 in logged/grazed forest 12 in burned forest 12 in abandoned road 10 in primary forest	Primary v. disturbed forest	Adult (>0.5cm dbh) plant species richness, density, basal area, mean number of stems/individual Saplings (<0.5 cm diameter; seed and adult plant sprouts) density and richness	Sapling density highest in logged forest due to one shrub species abundant in disturbed areas. Saplings of one species abundant at all site because of sprouting ability	Methodology: No replication	Yes – sapling species data in logged v. primary forest
Teketay (1997)	Afromontane forest in Ethiopia 1200 mm annual rainfall with wet period Between June and September	Two forest sites (one with selective removal of <i>Juniperus</i> ; the other with enrichment planting). 19x5m quadrats every	Regeneration along altitudinal gradient, separated by shade and gap.	Height class distribution of seedlings and number of seedlings of each species in each size class aggregated for	1 out of 4 species showed more rapid height growth in gaps than under shade, other three had similar growth rates	Ecological characteristics: Extent of disturbance/enrichment Methodology: Altitude confounds	Maybe? – shade/gap mortality and growth separation and positive/negative growth BUT only

	and a less pronounced wet period in March and April	50m altitudinal change – 46 and 11 in the two sites		shade and gap Mortality and proportion of selected species in shade/gap and evidence of competition /facilitation		aggregated shade/gap results	for four species Contact author for primary data?
Toniato et al. (2004)	Southeastern Brazil Total rainfall unclear – 250mm monthly Dec-Jan-Feb and 50mm monthly May-June-July	2 undisturbed forest stands, and 2 disturbed forest stands (cut and regarzed and abandoned 40 years ago) combined with either occasional or intense cattle trampling. 4 plots 40m x 40m in each stand	Secondary and primary forest (intense or occasional trampling)	Physiognomic features – no. individuals, basal area, height, abundance of climbing plants, canopy height, canopy gap area, no. dead trees Species classified into regeneration (pioneer, shade-tolerant climax, light-demanding climax) and dispersion (anemochorous, zoochorous, autochorous) guilds	Primary stands had taller trees and canopies, lower species diversity, higher abundance of autochorous and shade-tolerant climax species, and lower abundance of pioneer and light-demanding climax species Different densities of most abundant species (despite high proportion of shared species) Tree density and basal are similar between primary and secondary stands	Ecological characteristics: Time since disturbance No separation of sprouts and seedlings Difference in soil properties (measured) between primary and secondary stands Methodology: Pseudoreplication	Yes – number of individuals of species in primary and secondary forest
Uhl et al. (1982)	Moist forest >3500 mm						No – moist forest
Van Bloem et al. (2007)	Southwest Puerto Rico 860mm with wet season September – November (hurricane season)	Sprout development and mortality monitored six times over seven years on 1047 stems in 5 mature forest plots (0.01 – 1.44 ha) across a gradient of hurricane effects and	Before (i.e. immediately after the hurricane and before sprouts developed) and after hurricane effects across a gradient of damage.	Sprout mortality (numbers) between species	Sprouting rate 3-fold higher and proportion of sprouting stems higher than before the hurricane Mortality of	Methodology: No replication Different plot sizes Only one plot used for 'before' dynamics	Yes - long-term data of species survival between species

		wind exposure	Before in largest plot only.		sprouting stems same as for non-sprouting stems after 7 years Sprout growth and survival varied among species		
Vieira et al. Biotropica (2006)	Central Brazil 1236 +/- 50 mm (SE) with 89% of the precipitation falling October - March	Seedlings of 7 tree species planted in 4 forest fragments (unlogged, lightly logged, heavily logged and heavily logged and burned) in gap and understorey with and without presence of cattle	Disturbed v. undisturbed forest and gaps v. shade and trampled v. untrampled (factorial)	Seedling survival and growth after 1 year	Survival similar in gaps and understorey in minimally disturbed forest, but lower in gaps of heavily disturbed forest Growth much higher in gaps than in understorey in minimally disturbed forests, but similar in heavily disturbed forest	Ecological characteristics: Should be minimal as seedlings were planted	Yes – facilitation data
Vieira et al. JTE (2006)	Central Brazil 1236 +/- 255 mm (SD) with 89% of the precipitation falling October - March	One area of early succession forest (8y-o; then cleared and ploughed); one 10 y-o pasture; one 25 y-o pasture. 30 plots of 10 x 10m in each cleared area. Trees >5 cm dbh sampled in 2.4 ha in forest fragment	Forest fragment v. cut forest and 10 y-o pasture and 25 y-o pasture	Relative abundance (%) of individuals of each species sprouting Species richness Similarity indices between forest fragment and cleared sites	Resprouting ability is a conspicuous functional trait of tropical dry forest tree species, even after long periods of disturbance	Ecological characteristics: Different histories of clearance and ploughing in sample areas Time elapsed since previous disturbance Time elapsed between disturbance and assessment	Yes – species compositional change data